

Immatures of the Old World Oil-Collecting Bee *Ctenoplectra cornuta* (Apoidea: Apidae: Apinae: Ctenoplectrini)

JEROME G. ROZEN, JR.¹

ABSTRACT

The mature oocyte, all five larval instars, and the pupa of *Ctenoplectra cornuta* Gribodo are described based upon specimens from Taiwan. Its mature larva though larger is compared with, and found similar to, that of the African *Ctenoplectra armata* Magretti, the only other larval ctenoplectrine studied to date. The egg index was similar to that of the African *C. albolimbata* Magretti. Although *Ctenoplectra* shares certain larval and pupal similarities with *Tetrapedia* (Tetrapediini), a broader study including representatives of all apine tribes needs to be considered for evaluating tribal relationships.

INTRODUCTION

Offered here are descriptions of the mature oocyte, larval instars, and pupa of *Ctenoplectra cornuta* Gribodo in anticipation that these data may eventually be helpful in establishing the correct placement of the tribe Ctenoplectrini within the subfamily Apinae. Of approximately 20 species assigned to the two genera of the tribe, the mature larva of only *Ctenoplectra armata* Magretti was described earlier (Rozen, 1978) as was the mature oocyte of *C. albolimbata* Magretti (Rozen, 2003). No ctenoplectrine pupa has been treated before. Added also is information on larval development and a few observations on nesting biology. All specimens

¹Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024 (rozen@amnh.org).

studied became available through I-Hsin Sung's research on the nesting biology of the genus (Sung et al., 2009).

The familial placement of *Ctenoplectra* and related *Ctenoplectrina* was uncertain until Roig-Alsina and Michener (1993) and Silveira (1993) undertook phylogenetic studies that indicated that *Ctenoplectra* fell well within Apinae (Apidae) (Michener, 2007). This conclusion was supported by discovering that female *Ctenoplectra albolimbata* Magretti has four ovarioles per ovary, as is uniquely characteristic of many Apidae (Rozen, 2003). In a consensus tree based on adult, non-cleptoparasitic taxa, Roig-Alsina and Michener (1993: analysis D) showed that the two genera branched separately in an eight-branched polytomy, and Silveira (1993) concluded: "In many of the trees obtained, Tetrapediini was the most primitive branch of the Apinae, and Ctenoplectrini was part of the 'eucerine' line; in other trees, these two tribes were the basal branches of the 'apine line.'" More recently Schaefer and Renner (2008: fig. 3) presented a maximum-likelihood phylogram that showed (1) Ctenoplectrini to be a sister to Eucerini and (2) Tetrapediini as a basal clade leading to the Ctenoplectrini/Eucerini lineage based on mitochondrial and nuclear data. They again showed this relationship of Ctenoplectrini and Eucerini in a subsequent study though in a somewhat more derived position in the family (Renner and Schaefer, 2010).

OVARIAN STATISTICS AND DESCRIPTION OF MATURE OOCYTE

Figure 1

The single female of *Ctenoplectra cornuta* available to be dissected had four ovarioles per ovary (i.e., ovarian formula 4:4) and a single mature oocyte that was at least as long as any of the other entire ovarioles. The female's intertegular distance was 3.00 mm, providing the specimen with an egg index of 0.56 (Iwata and Sakagami, 1966). Although this index falls in the *small* category (ibid.: table 2) that contrasts with the *dwarf* category egg index of *Ctenoplectra albolimbata* Magretti (Rozen, 2003), it is insignificantly higher than the 0.50 index of the latter species.

DIAGNOSIS: The mature oocyte of *Ctenoplectra cornuta* was similar externally to that of *C. albolimbata* (Rozen, 2003), but the micropylar area was too poorly preserved to determine whether distinctive features might be found there.

DESCRIPTION (fig. 1): Length 1.73 mm; maximum diameter 0.44 mm. Color white; chorion smooth when viewed with stereomicroscope. Shape strongly curved (perhaps due to being preserved before dissection from female), symmetrical around long axis, rounded at both ends with front end slightly smaller than rear end; micropyle at front end indistinctly discernable with stereoscope. As viewed with SEM chorion smooth, featureless except for small mound (presumably micropylar area) at anterior pole with indistinct cluster of pores surrounded by 4–5 radiating fissures.

MATERIAL STUDIED: One female, Taiwan: Chiayi Co.: Shuisheliao, March 25, 2009 (I-Hsin Sung).

MATURE LARVA

Figures 2–7

This account is based on two last-stage larvae, one of which was postdefecating, and the other a last larval instar that was approaching maturity but had not yet defecated. Three larval exoskeletons (obviously postdefecating forms) associated with pupae helped to interpret the mandible.

DIAGNOSIS: The mature larva of *Ctenoplectra cornuta* closely agrees with the postdefecating larva of *C. armata* (Rozen, 1978). The following description provides some features that were not recorded in the account of *C. armata* published more than 30 years ago because their possible significance had not yet been realized. Although there are slight differences in pigmentation

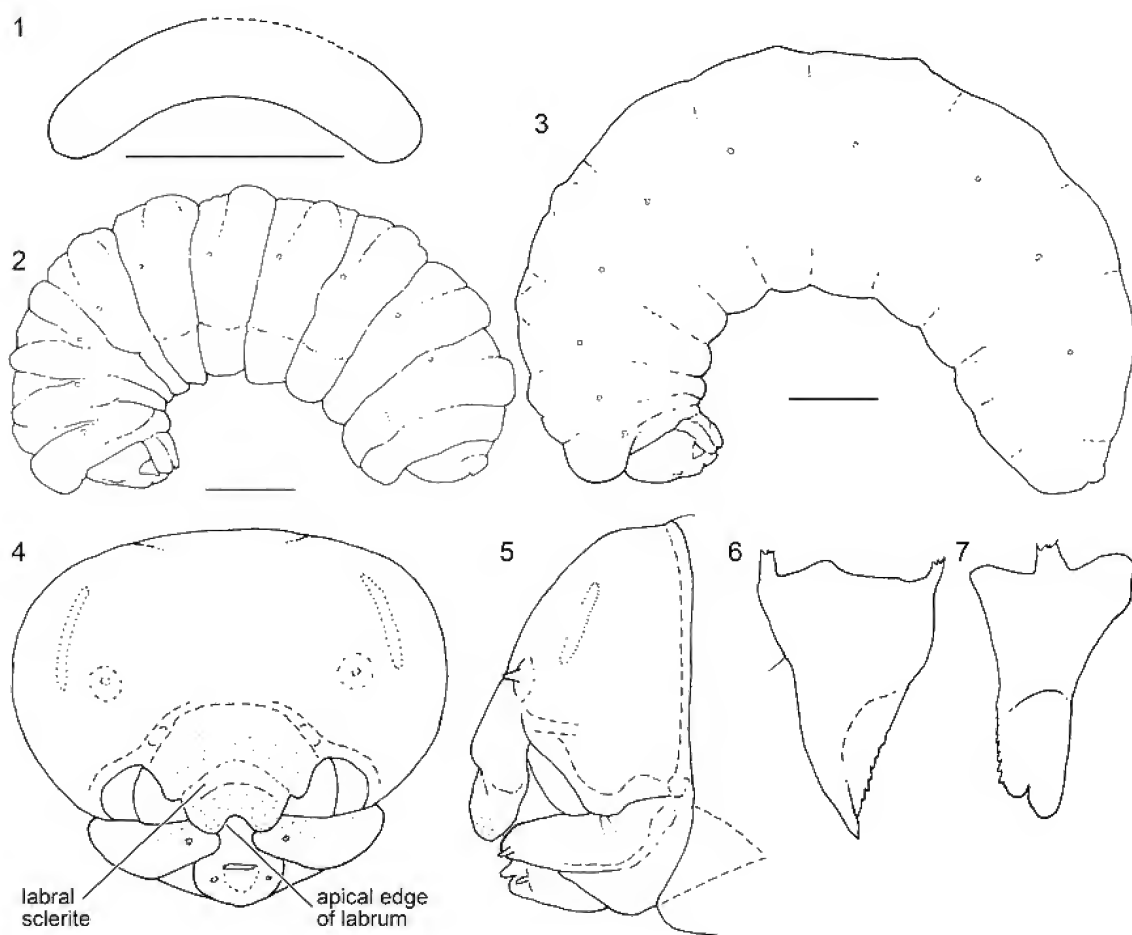


FIGURE 1. Camera lucida diagram of egg of *Ctenoplectra cornuta*, lateral view, with partial reconstruction of midbody indicated by interrupted line, anterior end to left. FIGURES 2–7. Last larval instars of *Ctenoplectra cornuta*. 2. Postdefecating larva, lateral view. 3. Predefecating larva, lateral view. 4, 5. Head of latter, frontal and lateral views, respectively. 6, 7. Right mandible, dorsal and inner views, respectively. Scale lines under figs. 1–3 = 1.0 mm.

and spiculation between these two species, disparity in head capsule width seems to be the most reliable way to distinguish the two (statistics for *C. armata* given in Remarks, below).

The mature larvae of *Ctenoplectra* can be distinguished from those of most other known tribes of the Apinae because those of *Ctenoplectra* have the apical edge of the labrum broadly emarginated medially (fig. 4).

HEAD (figs. 4, 5): Integument of head capsule with scattered, small, setiform sensilla; integument without spicules except for hypopharynx and pair of spiculate patches on anterolateral part of epipharyngeal surface. Integument unpigmented except for mandibular apices, basal ridges of mandibles, and areas of head capsule articulating with mandibles.²

Head (figs. 2, 3) moderate in size compared to body size; head capsule strongly constricted behind; maximum transverse width 1.18 mm; maximum transverse foramen width 0.9 mm; hence, foramen to head index 0.76; head capsule much wider than length measured from top of vertex to lower clypeal margin in frontal view. Tentorium robust, complete, including dorsal arms. Center of anterior tentorial pit closer to anterior mandibular articulation than to antenna in frontal view (fig. 4); attachment of anterior tentorial arm to front of head large, conspicuous on cleared specimen; posterior tentorial pits in normal position; all internal head ridges strongly developed except median coronal ridge nearly absent and epistomal ridge between anterior tentorial pits much weaker than ridge laterad of pits but still evident on cleared specimen; dorsomedian portion of postoccipital ridge bending forward as viewed from above; hypostomal ridge without dorsal ramus. Parietal bands evident as integumental scars. Antennal prominence weak; diameter of antennal disc distinctly smaller than distance between anterior tentorial pit and disc; antennal papilla small but moderately long, with length more than twice basal diameter, tapering to rounded apex bearing approximately three, closely clustered sensilla. Labrum not strongly projecting in lateral view (fig. 5), apically strongly bilobed with the median area deeply recessed in frontal view (fig. 4); broad, unpigmented labral sclerite evident across base. Epipharyngeal surface finely spiculate under each labral lobe.

Mandible (figs. 6, 7, 15) short, robust, with rounded teeth of approximately equal width but ventral tooth somewhat longer than dorsal tooth; apical half of mandible broad, nearly parallel sided in inner or outer views (figs. 7, 15), scoop shape formed by broad apical concavity; dorsal edge of dorsal tooth serrate, not produced into cusp basally; dorsal edge of ventral tooth with single, similar serration; mandible without defined cusp,³ denticles, small teeth, or other features, except for single seta arising from small tubercle near base on outer surface. Labiomaxillary region weakly projecting (for cocoon-spinning larva) in lateral view (fig. 5) with labium projecting about as far as maxilla. Maxilla with apex bent adorally, bearing palpus subapically; cardo weakly sclerotized but strongly projecting laterally; stipes heavily scler-

² Because postdefecating larvae usually gradually develop pigmentation, one might assume that an older larva than the one examined might be more extensively pigmented. However, the two cast last larval instar skins seemed no darker than the one studied.

³ Although Rozen and McGinley (1974) defined various terms used in describing the mandible of a bee larva, definition of the "cusp" has remained elusive. As used here, it refers to the projecting (when viewed from above or below), broadened (when viewed aborally) basal area of the dorsal apical edge, often bearing teeth or denticles.

rotized;⁴ articulating arm of stipital sclerite well developed, pigmented; maxillary palpus small in diameter, nearly parallel sided, length about as long as antennal papilla. Labium strongly divided into prementum and postmentum, but premental sclerite only faintly evident laterally; labial palpus subequal in length to maxillary palpus. Salivary lips projecting, transverse, on apex of prementum. Hypopharynx with a pair of finely spiculate lobes well behind apices of articulating arms of stipes; hypopharyngeal groove essentially absent although presumably at apices of articulating arms of stipes.

BODY: Integument without general body setae as found in most Megachilidae but with scattered, fine, setiform sensilla in vicinity of anus and with extremely finely spiculate areas there and elsewhere visible only on cleared specimen with compound microscope. Body form (figs. 2, 3) moderately robust; intersegmental lines weakly incised on predefecating larva (fig. 3), deeply incised on postdefecating form (fig. 2); intrasegmental lines not evident on predefecating larva (fig. 3) but conspicuous on postdefecating larva (fig. 2); paired dorsal body tubercles faintly suggested on anterior body segments but not evident elsewhere on predefecating larva (fig. 3); low paired tubercles present on most body segments on postdefecating larva (fig. 2); these tubercles so low that in lateral view, caudal annulet appearing only slightly higher than cephalic annulet; abdominal segment 9 not produced ventrally, so that ventral outline of terminal body segments continuous on predefecating form, as in figure 3; abdominal segment 10 positioned centrally on 9 in lateral view (fig. 3);⁵ anus positioned close to dorsal surface on segment 10 (figs. 2, 3). Spiracles (figs. 2, 3, 12) small, subequal throughout, not surrounded by sclerites, and not on tubercles; peritreme present but difficult to detect because integument very thin; atrium projecting slightly beyond body wall, with rim, globose; atrial wall smooth, without ridges or spines, moderately thick; primary tracheal opening with collar that does not project deeply into atrium; subatrium normal in length, consisting of about 7–8 chambers decreasing in diameter from body surface inward. Sex characters unknown (but see Remarks, below).

MATERIAL STUDIED: One postdefecating and one predefecating last larval instar, Taiwan: Nantou: Sitou, VI-22-08 (I-Hsin Sung); one cast postdefecating exoskeletons, same data; two cast postdefecating exoskeletons, same data except VIII-07-2008.

REMARKS: For *Ctenoplectra armata* the maximum transverse head width was 0.88 mm (considerably less than the 1.18 mm of *C. cornuta*) and the maximum transverse foramen width was 0.69 mm, yielding a foramen to head index of 0.78 nearly the same as that of *C. cornuta*.

Although the description of the mandible, given above, was based on the predefecating last instar, it suffices for the mandibles on the postdefecating larva and on the cast exoskeleton of the postdefecating larva. Nonetheless, the mandibular apex of all postdefecating exoskeletons shows considerable wear in that the two apical teeth are shorter and appear more fused, and the serrations on the dorsal apical edge are abraded particularly toward the apex of the tooth. Mandibular wear is a broad-ranging phenomenon among last stage, pollen-feeding aculeate

⁴ A reexamination of the larva of *Ctenoplectra armata* shows that its cardo and stipes are essentially identical to those of *C. cornuta* contrary to Rozen's (1978) description of the cardo as "well sclerotized".

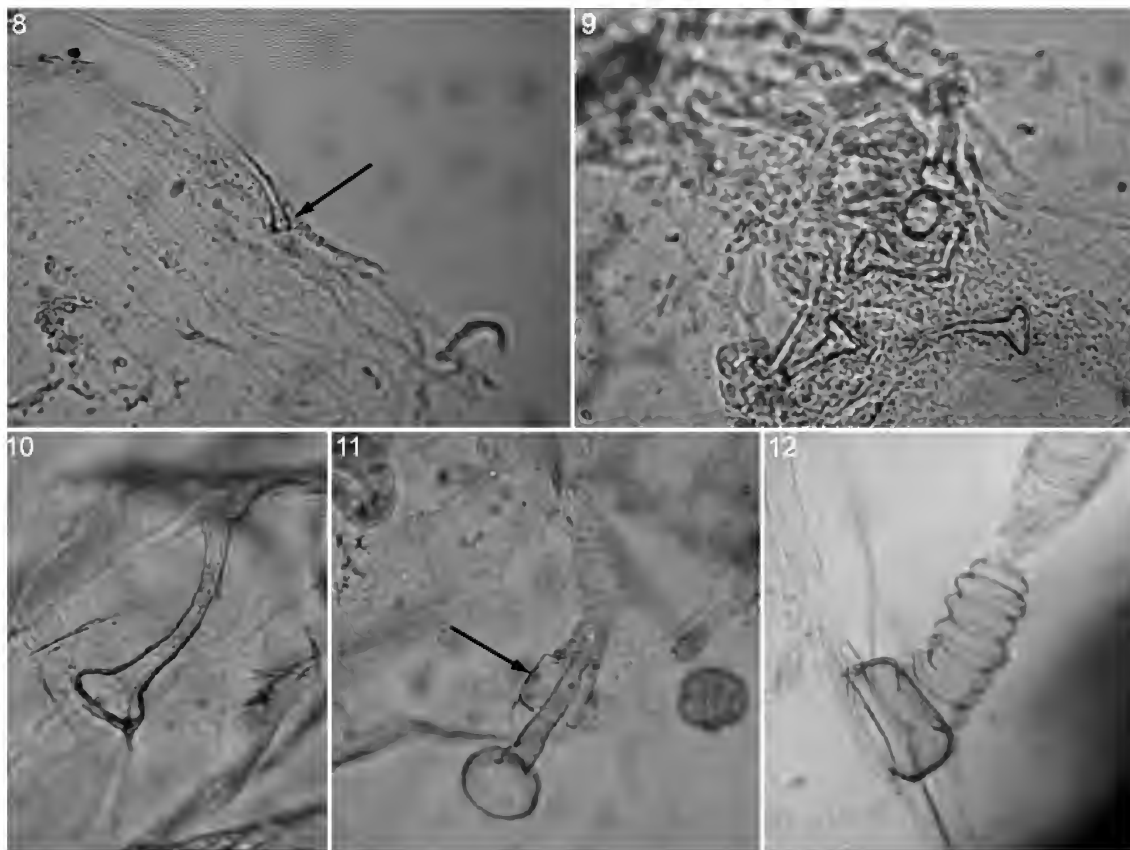
⁵ Specimen of the postdefecating larva illustrated (fig. 2) may have been preserved poorly, so that the rear of body may be misshapen.

larvae recently discussed with respect to *Stelis* (Megachilidae) (Rozen and Kamel, 2009b) and to the cleptoparasitic wasp *Sapyga* (Sapygidae) (Rozen and Kamel, 2009a).

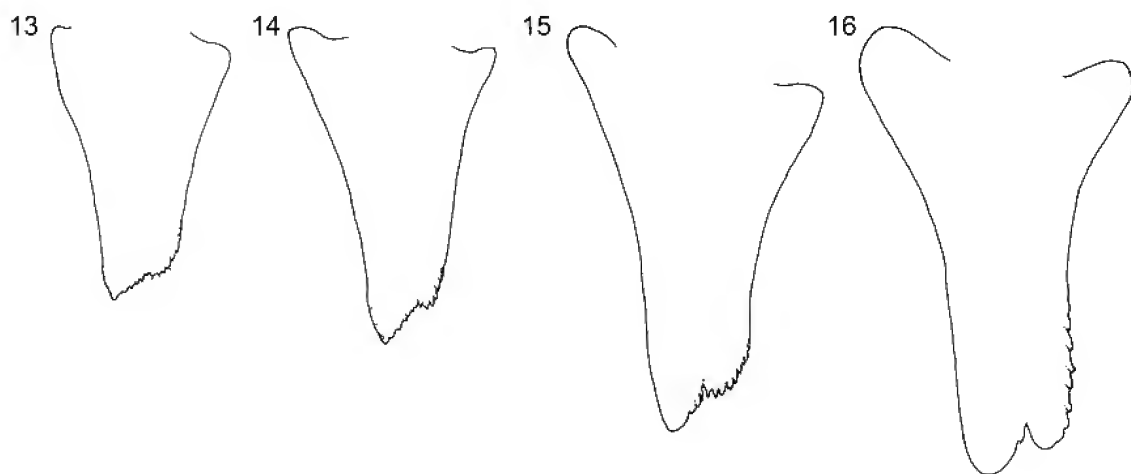
In general, the male sex character of last-stage bee larvae is a median integumental scar toward the posterior end of abdominal segment 9, as identified in the larva of *Ctenoplectra armata* (Rozen, 1978). Female sex characters are usually a pair of imaginal discs occasionally visible through the venter of abdominal segments 7–9, often without associated integumental deformities. On the two cleared specimens of *Ctenoplectra cornuta*, the absence of a median integumental scar on the venter of abdominal segment 9 implies that both were female.

OTHER LARVAL INSTARS

When the predefecating last instar was collected, an intermediate stage larva was discovered with exoskeletons of three earlier instars attached to its venter, thus indicating that the intermediate stage larva was the fourth larval instar. Accordingly, *Ctenoplectra cornuta* has five



FIGURES 8–12. Microphotographs of spiracles of all five larval instars of *Ctenoplectra cornuta*, all to the same scale, showing progressive changes in morphology. 8. First instar (arrow). 9. Second instar. 10. Third instar. 11. Fourth instar. 12. Fifth instar.



FIGURES 13–16. Diagrams of outer surface of right mandibles of larval instars two through five of *Ctenoplectra cornuta*, all drawn to the same scale; instars two, three, and four are the same individual.

larval instars, the typical number for bees (e.g., Baker, 1971; Park, 1946; Alves-dos-Santos et al., 2002; Rozen et al., 2006; Rozen and Kamel, 2007).

The head capsule of the first instar is weakly sclerotized (probably an indication that the first instar is pharate in the egg chorion and that the second instar starts feeding on provisions, as noted by Alves-dos-Santos et al., 2006, and Rozen et al., 2006) in contrast to the well-sclerotized head capsule of subsequent instars, and the mandibles could not be identified on its cast exoskeleton. The exoskeleton of the first instar, however, can be recognized by its spiracles, each of which consists of a long, nearly parallel-sided tube (fig. 8) that is slightly more sclerotized than the body integument. At the body surface the end of the tube is slightly expanded into what eventually develops into the atrium of the last larval stage. The remainder of the tube develops through intervening instars into the subatrium of the fifth instar.

In the second and third instars, the exoskeletons clearly have distinctly sclerotized head capsules. The spiracles (figs. 9, 10) have widened apically into funnellike openings on the body surface, and the future subatrium tapers slightly as it progresses inward. The mandible of the second instar (fig. 13) ends in a single, sharply pointed apex, and the incipient dorsal tooth is a broad, rounded lobe above the sharp apical tooth, their separation being a shallow notch in the broad upper apical mandibular margin. The entire apical margin is coarsely serrate with small, apically directed, sharply pointed teeth. The ventral apical edge of the mandible bears irregular teeth that are finer than those along the apical edge. The apical concavity is evident and close to the mandibular apex compared with its position in the fifth instar. The mandible of the third instar is similar to that of the second but more attenuate, the dorsal apical tooth more defined, and ventral apical edge with the fine teeth now appearing as mere irregularities.

In fourth-instar spiracles (fig. 11), known from the entire specimen, the atrium assumes a more globular shape and for the first time the subatrium shows subatrial chambers forming.

Interestingly, because the larva was approaching its next ecdysis, figure 11 reveals the formation of the spiracle of the last larval instar (arrow) surrounding the base of the subatrium of the fourth instar. The microphotograph suggests that the atrium has a peritreme and shows a dark pollen grain to the right of the spiracle. The function of the variously modified openings to tracheal systems of bee larvae presumably is to exclude foreign bodies from entering the system. One likely foreign body, of course, is pollen. As can be determined from this picture, the presumed peritreme would indeed prevent entrance of this pollen grain.

The mandible of the fourth instar clearly demonstrated that the individual was approaching its last larval stage when preserved; the mandible of the fifth instar was developing in the mandible of the fourth (fig. 15). Because it was approaching molting, the mandibular exoskeleton had become soft, so that figure had to be partly reconstructed to correct distortion caused by clearing the specimen in an aqueous solution of sodium hydroxide. The microphotograph of the specimen (fig. 17) clearly shows the developing fifth-instar mandible within the mandible of the fourth.

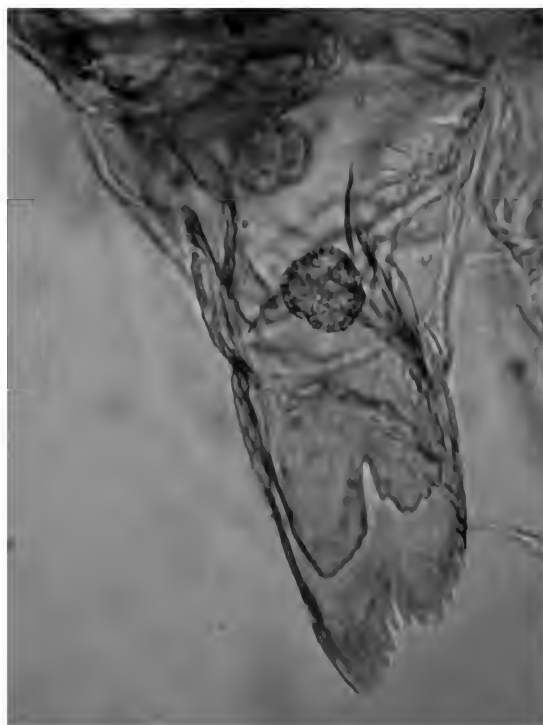


FIGURE 17. Microphotograph of mandible of fourth instar of *Ctenoplectra cornuta* showing developing mandible of fifth instar within it.

PUPA

Figures 18–22

DIAGNOSIS: Bee pupae are poorly known compared even with mature larvae of bees. However, the absence of paired mesoscutal and/or mesoscutellar tubercles and of tegular tubercles in pupal *Ctenoplectra cornuta* contrasts with described pupae of non-corbiculate, non-cleptoparasitic Apinae (Camargo et al., 1975; Cardale, 1968; Michener, 1954 [and references therein]; Rozen and Buchmann, 1990; Rozen and Michener, 1988; Rozen et al., 2006). The single exception is the pupa of *Tetrapedia diversipes* Klug (Tetrapediini) (Alves-dos-Santos et al., 2002), a genus and tribe found only in the New World. The pupa of *C. cornuta* can also be distinguished from all but one known pupal noncorbiculate cleptoparasitic Apinae (pupa of *Ctenoplectrina* unknown), which have paired mesoscutal and/or mesoscutellar tubercles and/or tegular tubercles (Rozen, 2000). That exception is the pupa of *Coelioxoides waltheriae* Ducke, also a representative of the New World Tetrapediini (Alves-dos-Santos et al., 2002); the pupal similarity of *Coelioxoides* and *Ctenoplectra* is treated further under Discussion.



FIGURES 18–19. Microphotographs of pupae of *Ctenoplectra cornuta*. 18. Female metasoma, ventral view. 19. Dorsal surface of male mesosoma showing small paramedian mesoscutal tubercles (double arrow), dorso-lateral view. Scale bars = 1.0 mm.

Because male and female pupae of *Ctenoplectra cornuta* show numerous differences, they are described separately.

FEMALE

Figures 18, 20, 21

DESCRIPTION: Length 7.4–9.4 mm; head and body without setae. **Head:** Scape and pedicel unmodified, without tubercles; each flagellomere tending to be swollen midlength with swellings increasing in size toward flagellar apex. Vertex with low tubercle over each ocellus and with scattering of fine tubercles accommodating apices of developing adult setae; elsewhere pupal integument of head without modification, but each paraocular area with large tubercle-like swelling accommodating large swelling on adult integument; labral apex extending well beyond that of adult, allowing development of long apical adult setae. Mandible without swellings or tubercles, ending in simple tapering apex, not reflecting subapical adult tooth. Proboscis without unusual features.

Mesosoma: Setae absent; integument unremarkable. Pronotum with lateral angle and lobe slightly produced; mesoscutum, mesoscutellum, axilla, metanotum, and propodeum without tubercles or large swellings; propodeal spiracle elongate with anterior medially directed, finely spiculate lobe. Tegula without tubercle, dorsal surface verrucose. All leg tubercles accommodating adult setae except those of adult spurs; fore-, mid-, and hind coxae each with long tapering spine on inner apical angle; all trochanters each with shorter apical spines; forefemur with basal spine on outer surface; midfemur with small basal spine; hind femur with small basal angle; fore- and midtibiae each with several small rounded apical tubercles; hind tibia greatly expanded apically (fig. 21) with large curved apical tubercle on outer (hind) angle; inner apical spur

enlarged basally (fig. 21), accommodating greatly modified adult structure; first four tarsomeres on foreleg apically enlarged and ending in several small tubercles; first tarsomere on midleg elongate, allowing development of long, stout, apically curved and thus rakelike adult setae perhaps used to manipulate floral oil; first segment of hind tarsus (fig. 21) enlarged to accommodate scopal setae; other tarsomeres similar to those of other legs; all tarsal claws a simple lobe, not showing cleft of adult claw.

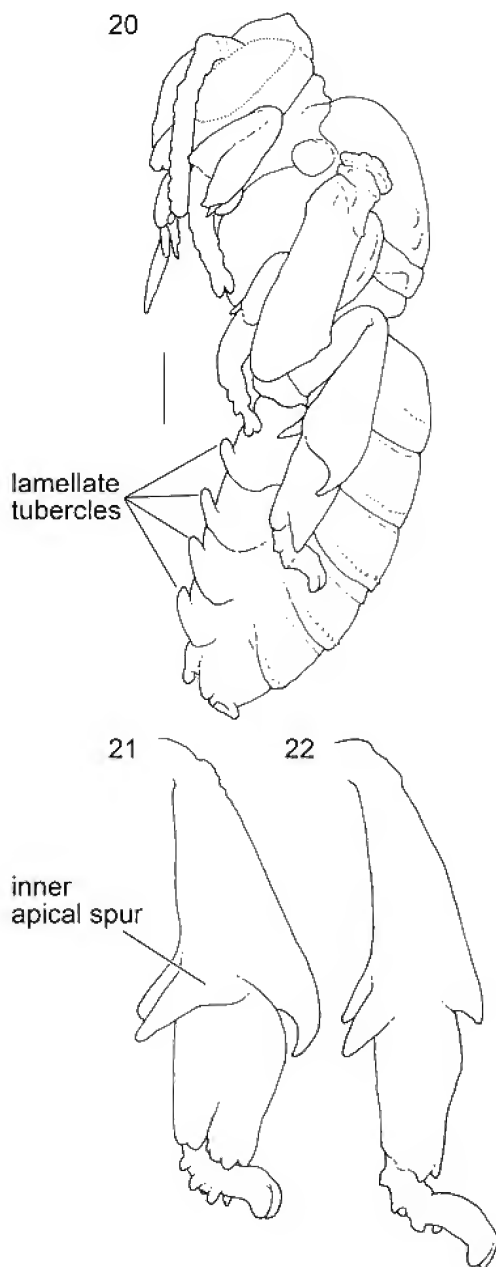
Metasoma: Terga I–V (fig. 20) each with subapical transverse rows of small, often sharply pointed tubercles, and often with sclerotized, pigmented apices; those of tergum I mostly smaller, less conspicuous than those of following segments; rows interrupted medially; tergum VI with only one or two small tubercles. Sternum I unremarkable; sterna II–V (fig. 20) each with inverted, more or less V-shaped, semierect lamellate tubercle traversing entire sternum, accommodating developing adult oil-collecting hairs (fig. 18). Terminal spine short, dorsoventrally flat, apically truncate to rounded as seen from above or below.

MALE

Figures 19, 22

DESCRIPTION: As described for female except for following: Length 6.7–9.3 mm. **Head:** Paracocular tuberclelike swelling not as pronounced as that of female.

Mesosoma: Mesoscutum with pair of minute tubercles (fig. 19). Forefemur with basal spine on outer surface; midfemur with small basal protuberance; hind femur with small basal angle; fore- and midtibiae each with several small, rounded apical tubercles; hind tibia not much expanded apically (fig. 22) compared to that of female, with apical tubercle on outer (hind) angle that is far less pronounced than that of female; inner apical tibial spur not expanded basally (fig. 22), not



FIGURES 20–22. Diagram of pupae of *Ctenoplectra cornuta*. **20.** Entire female pupa, lateral view showing overall shape; terminal spine compressed and therefore truncate in dorsal/ventral view. Scale bar = 1.0 mm. **21, 22.** Diagrams of right hind pupal tibia and tarsus, inner view, drawn to same scale, female and male, respectively.

enlarged like that of female; first tarsomere on midleg elongate like that of female but developing setae tapering, not apically curved and thus not rakelike; first segment of hind tarsus (fig. 22) about as long as that of female, but thinner.

Metasoma: Terga I–VI each with subapical transverse rows of small, often sharply pointed tubercles, and often with sclerotized, pigmented apices; rows interrupted medially; tergum VI with only one or two small tubercles. Sterna I–V unremarkable, without inverted, more or less V-shaped, transverse, semierect lamellate tubercle as in female.

MATERIAL STUDIED: Two female and two male pupae, Taiwan: Nantou: Sitou, June 22, 2008 (I-Hsin Sung); two male pupae, same data except August 7, 2008.

REMARKS: The pupae were in various stages of development; the darker ones were the most developed and the largest, suggesting that large size correlates with age. Pupal details were most easily observed on darker specimens.

DISCUSSION

A study (Alves-dos-Santos et al., 2002) in which larval exemplars of the two genera of Tetrapediini were described pointed out that both *Ctenoplectra* and *Tetrapedia* had basal labral sclerites (an uncommon feature elsewhere in the Apinae) as well as a number of other similarities. Although Tetrapediini (New World) and Ctenoplectrini (Old World) are completely allopatric, both are collectors of floral oils and are nonground nesters capable of using preformed cavities. Additionally, larvae of both share a short coronal ridge, a broad to moderately broad, scooped-shaped apical mandibular concavity, and both lack a mandibular cusp and a defined hypopharyngeal groove. In each, the venter of abdominal segment 9 does not protrude in lateral view. However, these features are encountered among other unrelated bee taxa, so that in final analysis, they do not seem to be particularly reliable indicators of a possible relationship of ctenoplectrines and tetrapediines.

Furthermore, *Ctenoplectra* and *Tetrapedia* have some striking differences: *Tetrapedia* larvae do not spin cocoons; their labium is narrowly pointed; the opening to the labial gland is a simple hole without transverse lips, situated dorsally on the prementum; and the anus is located in the middle of abdominal segment 10. In contrast, *Ctenoplectra* larvae spin cocoons; their labium, though fairly narrow, is apically rounded, bears projecting, apical, transverse salivary lips, and the anus is dorsally positioned on abdominal segment 10. Although the spiracles (relative to body size) of *Ctenoplectra* are moderately small (as is also the case for many other apine tribes), those of *Tetrapedia* are the smallest that the author has ever seen on a bee larva.

In addition to the mature larval anatomy of *Ctenoplectra* and *Tetrapedia*, it is now possible to compare pupal features. The pupae of *Ctenoplectra* (fig. 20) and Tetrapediini (i.e., both *Tetrapedia* and *Coelioxoides*) (Alves-dos-Santos et al., 2002: figs. 57, 58) seem similar because of the absence (except for pair of minute tubercles in male, fig. 19) of dorsal mesosomal tubercles. In sharp contrast, published pupal descriptions of exemplars of all other non-cleptoparasitic, non-corbiculate apine tribes have conspicuous tubercles (Masuda, 1946; Michener, 1954; Cardale, 1968; Mohamed, 1974; Camargo et al., 1975; Rozen and Michener, 1988; Rozen and Buchmann, 1990; Rozen et al., 2006), as is also true for published accounts of all cleptoparasitic apid

taxa except for the Nomadinae (Rozen, 2000, and references therein; Rozen et al., 2006). The absence of these tubercles in *Ctenoplectra* and Tetrapediini may or may not be evidence that they had a common ancestor lacking such tubercles (instead they might have evolved independently from common nesting requirements).

For the present, the relationships of Ctenoplectrini to the other tribes of the Apinae remain uncertain when evaluated on the basis of mature larvae and pupae. A comprehensive comparative study of immatures of all tribes may be helpful in illuminating tribal interrelationships in the future.

BIOLOGICAL NOTES

With the immatures of *Ctenoplectra cornuta*, I-Hsin Sung provided fragments of the cells and cocoons that offer insight into the nesting biology of the species not included in his treatment of its biology (Sung et al., 2009). These fragments show that fresh cell walls are smooth, and at least some are covered with a dark, shiny material, as reported by Sung et al. (2009); cell walls that were less reflective may have belonged to earlier generations. When tested with water droplets placed on the inner surface of the fresh wall and on unworked broken surfaces, both surfaces were hydrofuge, probably indicating impregnation by floral oils either at the time of soil collection or during cell construction. The inner surface of the cell closure, 3.5–4.2 mm in diameter ($N = 7$) is a more or less distinct, nearly flat to moderately concave spiral of three coils to the radius (fig. 23). The outer surface is concave and smooth.

Feces of *Ctenoplectra cornuta* in some cases are appressed against the rear part of the cell. Cocoons consist of a single thin layer of silk forming a semitransparent sheet that adheres closely to the cell wall and to the feces at the cell rear (thus indicating the defecation is completed before spinning). The silk strands fuse while being deposited, since no single strand is in evidence and the cocoon inner surface is reflective like cellophane.

Fragments of the cell lining of *Ctenoplectra chalybea* Smith (Taiwan: Hsinhua VIII-2008) also provided by Sung were similar to those of *C. cornuta*. Their fragments were coated with a semitransparent, waxy substance (as also mentioned by Sung et al., 2009) that when scraped with forceps left a shiny streak as would wax. Beneath, the waxy material penetrated the soil in some places by 0.5 mm and elsewhere perhaps much more. The surface waxy layer and the penetrated soil were much darker than the surrounding soil.



FIGURE 23. Microphotograph of brood cell closure, showing spiral configuration.

ACKNOWLEDGMENTS

I extend my sincere thanks to I-Hsin Sung, who collected and generously shared all specimens of *Ctenoplectra cornuta* used in this study.

S.E.M. examination of specimens was performed in the AMNH Microscopy and Imaging Facility (Rebecca Rudolph, Laboratory Manager) with the technical assistance of Matthew Frenkel. Steve Thurston, Senior Scientific Assistant, AMNH, expertly prepared the illustrations for publications.

I thank I-Hsin Sung and two anonymous outside reviewers who have kindly read this manuscript.

REFERENCES

- Alves-dos-Santos, I., G.A.R. Melo, and J.G. Rozen, Jr. 2002. Biology and immature stages of the bee tribe Tetrapediini (Hymenoptera: Apidae). *American Museum Novitates* 3377: 1–45.
- Baker, J.R. 1971. Development and sexual dimorphism of larvae of the bee genus *Coelioxys*. *Journal of the Kansas Entomological Society* 44: 225–235.
- Camargo, J.M.F. de, R. Zucchi, and S. Sakagami. 1975. Observations on the bionomics of *Epicharis (Epicharana) rustica flava* (Olivier) including notes on its parasite, *Rhathymus* sp. (Hymenoptera, Apoidea: Anthophoridae). *Studia Entomologica* 18: 313–340.
- Cardale, J. 1968. Immature stages of Australian Anthophorinae (Hymenoptera: Apoidea). *Journal of the Australian Entomological Society* 7: 35–41.
- Danforth, B.N., S. Sipes, J. Fang, and S.G. Brady. 2006. The history of early bee diversification based on five genes plus morphology. *Proceedings of the National Academy of Sciences* 103: 15118–15123.
- Iwata, K., and S.F. Sakagami. 1966. Gigantism and dwarfism in bee eggs in relation to the mode of life, with notes on the number of ovarioles. *Japanese Journal of Ecology* 16: 4–16.
- Masuda, H. 1946. Biological notes on *Eucera difficilis* Perez and whose [sic] parasitic bee, *Nomada japonica* Smith, with descriptions of a gynandromorphic *Eucera*. *Kontyu* 14: 45–60.
- Michener, C.D. 1954. Observations on the pupae of bees. *Pan-Pacific Entomologist* 30: 63–70.
- Michener, C.D. 2007. *Bees of the world*. Baltimore, MD: Johns Hopkins University Press. 953 pp.
- Michener, C.D., and L. Greenberg. 1980. Ctenoplectridae and the origin of long-tongued bees. *Zoological Journal of the Linnean Society* 69: 183–203.
- Mohamed, M.R. 1974. Seasonal distribution of *Tetralonia lanuginosa* Klug with a taxonomic description of different stages (Hym., Anthophoridae). *Deutsche Entomologische Zeitschrift* 21: 167–178.
- Park, O.W. 1946. The honeybee colony—life history. In R.A. Grout (editor), *The hive and the honeybee*: 62–124. Hamilton, IL: Dadant.
- Renner, S.S., and H. Schaefer. 2010. The evolution and loss of oil-offering flowers: new insights from dated phylogenies for angiosperms and bees. *Philosophical Transactions of the Royal Society Biological Sciences* 365: 423–435.
- Roig-Alsina, A., and C.D. Michener. 1993. Studies of the phylogeny and classification of long-tongued bees (Hymenoptera: Apoidea). *University of Kansas Science Bulletin* 55: 123–162.
- Rozen, J.G., Jr. 1978. The relationships of the bee subfamily Ctenoplectrinae as revealed by its biology and mature larva (Apoidea: Melittidae). *Journal of the Kansas Entomological Society* 51: 637–652.
- Rozen, J.G., Jr. 2000. Pupal descriptions of some cleptoparasitic bees (Apidae), with a preliminary generic key to pupae of cleptoparasitic bees (Apoidea). *American Museum Novitates* 3289: 1–19.

- Rozen, J.G., Jr. 2003. Ovarian formula, mature oocyte, and egg index of the bee *Ctenoplectra* (Apoidea: Apidae). *Journal of the Kansas Entomological Society* 76: 640–642.
- Rozen, J.G., Jr., and S.L. Buchmann. 1990. Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). *American Museum Novitates* 2985: 1–30.
- Rozen, J.G., Jr., and S.M. Kamel. 2007. Investigations on the biologies and immature stages of the cleptoparasitic bee genera *Radoszkowskiana* and *Coelioxys* and their *Megachile* hosts (Hymenoptera: Apoidea: Megachilidae: Megachilini). *American Museum Novitates* 3573: 1–43.
- Rozen, J.G., Jr., and S.M. Kamel. 2009a. Hospicidal behavior of the cleptoparasitic wasp *Sapyga luteomaculata* and investigation into ontogenetic changes in its larval anatomy (Hymenoptera: Vespidae: Sapygidae). *American Museum Novitates* 3644: 1–24.
- Rozen, J.G., Jr., and S.M. Kamel. 2009b. Last larval instar and mature oocyte of the old world cleptoparasitic bee *Stelis murina*, including a review of *Stelis* biology. (Apoidea: Megachilidae: Megachilinae: Anthidiini). *American Museum Novitates* 3666: 1–24.
- Rozen, J.G., Jr., and R.J. McGinley. 1974. Phylogeny and systematics of Melittidae based on the mature larvae (Insecta, Hymenoptera, Apoidea). *American Museum Novitates* 2545: 1–31.
- Rozen, J.G., Jr., and C.D. Michener. 1988. Nests and immature stages of the bee *Paratetrapedia swainsonae* (Hymenoptera: Anthophoridae). *American Museum Novitates* 2909: 1–13.
- Rozen, J.G., Jr., G.A.R. Melo, A.J.C. Aguiar, and I. Alves-dos-Santos. 2006. Nesting biologies and immature stages of the tapinotaspidine bee genera *Monoeca* and *Lanthanomelissa* and of their osirine cleptoparasites *Protosiris* and *Parepeolus* (Hymenoptera: Apidae). *American Museum Novitates* 3501: 1–60.
- Schaefer, H., and S.S. Renner. 2008. A phylogeny of the oil bee tribe Ctenoplectrini (Hymenoptera: Anthophila) based on mitochondrial and nuclear data: evidence for Early Eocene divergence and repeated out-of-Africa dispersal. *Molecular Phylogenetics and Evolution* 47: 799–811.
- Silveira, F.A. 1993. Phylogenetic relationships of the Exomalopsini and Ancylini (Hymenoptera: Apidae). *University of Kansas Science Bulletin* 55: 163–173.
- Sung, I., A. Dubitzky, C. Eardley, and S. Yamane. 2009. Descriptions and biological notes of *Ctenoplectra* bees from southeast Asia and Taiwan (Hymenoptera, Apidae, Ctenoplectrini), with a new species from North Borneo. *Entomological Science* 12: 324–340.

Complete lists of all issues of *Novitates* and *Bulletin* are available on the web (<http://digitallibrary.amnh.org/dspace>). Inquire about ordering printed copies via e-mail from scipubs@amnh.org or via standard mail from:

American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024

☉ This paper meets the requirements of ANSI/NISO Z39.48-1992 (permanence of paper).